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Seasonal Distribution, Trophic Structure and Origin of Sand Obligate Insect Communities in the Great Basin

R. W. Rust

Biology Department, University of Nevada, Reno, Nevada.

Recent surveys of insects in western North American sand dunes (Hardy and Andrews, 1979, 1981; Andrews et al., 1979; Cobb, 1981; Bechtel et al., 1981, 1983; Rust et al., 1983) have established the presence of unique, often endemic groups of Coleoptera, Hemiptera and Orthoptera. These species are referred to as sand obligate species and are defined as species whose life history activities are restricted to sand dune environments (Koch, 1961; Hardy and Andrews, 1976). I will show that sand obligate (SO) species from one sand dune, Sand Mountain, Nevada, are principally detritivores and carnivores that occur either throughout the year or in cold, winter months. The distribution of sand obligate faunas in several dunes in the Great Basin Desert of the United States may possibly be explained by examination of past climatic conditions during the Pleistocene in the Great Basin. The hypothesis being examined is that the present distributions and restriction of the sand obligate fauna is a result of contraction of Pleistocene sand areas with decreasing aridity in recent times.

Study Area

Sand Mountain dune is approximately 46 km ESE of Fallon, Churchill County, Nevada (39°20′N–118°20′W) and is 1250 m in elevation. It is an active star dune of approximately 3.2 km^2 and results from eolian sand deposited during the Turupah and Fallon formations of about 4000 years before present (B.P.) (Morrison and Frye, 1965). Sparse dune vegetation consists of the shrubs *Atriplex confertifolia, Tetradymia tetrameres, Chrysothamnus viscidiflorus, Eriogonum kearneyi, Psorothamnus polyadenius* and the grass *Oryzopsis hymenoides.* The dune was sampled 18 times from June 1979 through June 1980.

Monthly average temperature and precipitation from Fallon, Nevada (39°27′–118°47′W and 1208 m elevation) for a thirty year period are given in Table 1 (USDC 1970). Sand Mountain is in the cold desert of North America with cold, wet winters (−0.4 to 5.8°C and 1 to 1.6 mm) and hot, dry summers (10 to 22°C and 0.5 to 1.8 mm). Thirty year mean monthly temperatures were analyzed by Fisher's L.S.D. test to determine which months have equal mean temperatures. L.S.D. valve was 0.73°C or all monthly means are significantly different from each other.

Methods and Materials

Several collecting techniques were used. Permanent pitfall traps were 0.95 L (11.5 cm diameter) plastic cartons buried level with the sand surface and one-third to one-half filled with ethylene glycol. Traps were covered with a 13 × 13 cm Masonite lid held 2 cm above the surface. Six traps were placed 10 meters apart in a transect and six transects were used. Traps were operative for 30 days between collecting periods. Temporary pitfall traps were 15 cm diameter ceramic bowls placed level with the sand surface. Twelve traps placed 10 meters apart represented a transect and six transects were used. Temporary pitfall traps were used for 12 to 18 hr during a survey period and trapping duration was determined by the length of the night. Hand held lamps were used in searching the dune for nocturnal species. Sand was sifted through two screens of 12 × 12 mm and 1.5 × 1.5 mm mesh to recover subsurface arthropods. Surface sand to a depth of 0.4 to 0.5 m both from beneath vegetation and open sand (non-vegetated areas) was sifted. During surveys, four or five different sites on the dune were visited and sampled and the sites were varied each survey.

All specimens were sent to taxonomists for identification (see Bechtel et al., 1981, 1983; Rust et al., 1983 for listings). Four of the species were determined as new to science. These species will be described by taxonomists and are here treated as species unique to Sand Mountain, NV.

Trophic level placement of species was based on field observations, dissection of digestive tracts and literature citations. When few specimens were available or species specific literature was not available, then trophic level assignment was based on generic patterns.

Spearman's rank correlation test was used to compare a species monthly abundance to both mean monthly temperature and precipitation. The hypothesis being tested is that a species monthly abundance ranking is independent of either monthly temperature or precipitation ranking.

RESULTS

Sixteen species are recognized as sand obligate, 3 herbivores, 4 carnivores and 9 detritivores (Table 1). *Serica* species (Scarabaeidae) adults were found from May to June and were observed feeding of *Psoralea lanceolata* (Fabaceae) and *Ambrosia acanthicarpa* (Asteraceae). Larvae were recovered in October and March–April from sand beneath the roots of *Oryzopsis hymenoides* (Poaceae). Their guts contained masticated plant material. *Cardiophorus* species (Elateridae) adults were found from November to March and were recovered from sand beneath several dune shrubs. A single larva was taken in May. *Cardiophorus* have unknown feeding habits. The larval mouth opening is small suggesting that they probably take only liquid food. *Edrotes ventricosus* (Tenebrionidae) was present in all months but November to January. La Rivers (1947) observed *E. ventricosus* feeding on saltgrass, *Destichlis spicata,* brome grass, *Bromus tectorum,* Russian Thistle, *Salsola kali,* and wild onion, *Allium* sp. and considered it a strict herbivore. SO carnivores, *Rhadine myrmecodes* (Carabidae), and *Mecynotarsus delicatulus* (Anthicidae) were present in all months, *Philothris* species (Histeridae) was found during the winter months, and *Tetragonoderus pallidus* (Carabidae) was present from May to September. Of the detritivores, *Niptus ventriculus* (Ptinidae) (Hinton, 1941; Brown, 1959), *Eusattus muricatus* (Doyen, 1984 for recent review), *Lariversius tibialis* (gut analysis, unpublished data), and *Trogloderus costatus* (La Rivers, 1946; Tanner and Packham, 1965; Thomas, 1979) (Tenebrionidae) were present in all months. *Chilometopon brachystomum* (Doyen, 1982) (Tenebrionidae) was present during the summer months. *Aegialia hardyi* (Rust and Hanks, 1982), *Aphodius nevadensis* (gut analysis, unpublished data), and *Coenonycha* species (Scarabaeidae) were

Table 1. Seasonal distribution of sand obligate insects from Sand Mountain, Nevada from June 1979 through June 1980, larval numbers are given in parentheses. Species dry weight is given in milligrams (E means estimated dry weight because of few specimens). Mean monthly temperature and precipitation based on a thirty year average are given for Fallon, Nevada.

Species	Weight	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
					Herbivores								
Cardiophorus species	6.0E	2		1		(1)						1	2
Serica species	14.8			(17)	(37)	36	63	37			(10)		
Edrotes ventricosus	13.7		4	3	19	5	19	46	5	4	1		
					Carnivores								
Mecynotarsus delicatulus	5.0	3	2	5	2	2	7	12	296	26	9	3	1
Rhadine myrmecodes	94.0	2	21	29	7	13	12	7	25	12	1	13	22
Tetragonoderus pallidus	18.5					1	10	13	14	4			
Philothrus species	2.0E	1		2	2	4				2	2	1	
					Detritivores								
Ammobaenetes lariversi	40.1	3	7	4	2	10	42	48	30	40	45	3	1
Niptus ventriculus	6.6	4	1	3	1	3	33	5	12	9	2	11	7
Aegialia hardyi	2.2	158	55	54	68	30					54	86	60
				(79)	(144)	(38)							
Aphodius nevadensis	5.4	15	28	23								5	16
				(26)	(21)								
Coenonycha species	10.0E	6	4										
Chilometopon brachystomum	20.0E						12						
Eusattus muricatus	133.0	2	10	29	14	7	6	98	372	85	22	6	3
Lariversius tibialis	19.1	16	39	32	23	15	50	70	482	241	76	7	12
Trogloderus costatus	18.9	3	3	3	9	13	35	52	25	210	2	2	1
					Average temperature °C								
		−0.4	3.0	5.8	9.7	14.2	18.5	22.7	21.2	16.9	11.0	4.6	0.7
					Average precipitation mm								
		12.4	16.0	13.9	9.6	18.5	11.4	4.8	4.3	5.5	10.6	9.1	11.6

Table 2. Spearman's rank correlation and probabilities of species monthly abundance to monthly temperature and monthly precipitation 30 year averages and probability levels. Rankings are from high to low for monthly species abundance, temperature and precipitation.

	Temperature			Precipitation	
Species*	n	r_s	P	r_s	P
Mecynotarsus delicatulus	12	0.805	$0.002 < P < 0.005$	−0.631	$0.02 < P < 0.05$
Neptus ventriculus	12	0.335	$0.20 < P < 0.50$	−0.482	$0.10 < P < 0.20$
Rhadine myrmecodes	12	−0.108	$P > 0.50$	0.136	$P > 0.50$
Tetragonoderus pallidus	5	0.80	$P = 0.20$	−0.90	$P > 0.10$
Ammobaenetes lariversi	12	0.797	$0.002 < P < 0.005$	−0.203	$P > 0.50$
Aegialia hardyi	8	−0.660	$0.05 < P < 0.10$	−0.482	$0.20 < P < 0.50$
Aphodius nevadensis	5	0.375	$P > 0.50$	0.825	$0.10 < P < 0.20$
Edrotes ventricosus	9	0.595	$0.10 < P < 0.20$	−0.412	$0.20 < P < 0.50$
Eusattus muricatus	12	0.715	$0.01 < P < 0.02$	−0.548	$0.05 < P < 0.10$
Lariversius tibialis	12	0.692	$0.01 < P < 0.02$	−0.475	$0.10 < P < 0.20$
Trogloderus costatus	12	0.795	$0.002 < P < 0.005$	−0.319	$0.20 < P < 0.50$

* *Cardiophorus* species, *Philothris* species, *Coenonycha* species and *Chilometopon brachystomum* were not analyzed because of limited number of specimens and *Serica* species and also *Coenonycha* species and *Chilometopon brachystomum* were not analyzed because of insufficient sample size for Spearman's rank correlation test.

found during the winter months. Larvae of *Aegialia hardyi* and *Aphodius nevadensis* were found from March to May in sand beneath dune vegetation. *Ammobaenetes lariversi* (La Rivers, 1948) (Rhaphidophoridae) adults and nymphs were found in all months with most individuals obtained from July to October.

Spearman's rank correlation of species monthly abundance to either monthly temperature or precipitation 30 year averages (Table 2) indicate that *Mecynotarsus delicatulus, Ammobaenetes lariversi, Eusattus muricatus, Lariversius tibialis,* and *Trogloderus costatus* were significantly, positively correlated with monthly temperatures and only *Mecynotarsus delicatulus* was significantly, negatively correlated with monthly precipitation. *Eusattus muricatus* shows a possible negative relationship with monthly precipitation.

Discussion

Three seasonal activity patterns exist in the sand obligate species: 1) continuous year-round, 2) summer-warm months, and 3) winter-cold months. Carnivores *Rhadine myrmecodes,* and *Mecynotarsus delicatulus,* and detritivores *Ammobaenetes lariversi, Niptus ventriculus, Eusattus muricatus, Lariversius tibialis,* and *Trogloderus costatus* are active year-round. Herbivores *Serica* species, and *Edrotes ventricosus,* carnivore *Tetragonoderus pallidus,* and detritivore *Chilometopon brachystomum,* are summer-warm month species, with *E. ventricosus* extending into the cooler winter months. Winter-cold month species are herbivore *Cardiophorus* species, carnivore *Philothrus* species, and detritivores *Aegialia hardyi, Aphodius nevadensis,* and *Coenonycha* species. Winter activity of *Cardiophorus* species may represent non-feeding adults that mate and deposit eggs during this period. Other populations of *Cardiophorus* species from Great Basin sand dunes show similar adult winter activity periods (Hardy and Andrews, 1976; E. C. Becker, pers. comm.).

Comparisons of seasonal activity patterns of other populations of SO species

(Table 3) are in general the same as Sand Mountain. Notable exceptions are *Tetragonoderus pallidus* showing gradually year-round activity in populations at decreasing latitude or reduced cold-winter months, *Niptus ventriculus* with reduced hot-summer month activity with decreasing latitude, and *Trogloderus costatus* showing a reduction in the winter–spring activity with decreasing latitude.

Year-round and winter-cold active SO species are responding to both the physical and biotic factors during the cold period. During the cold-month period, warming of surface and subsurface (10 to 15 cm) above ambient produced an environment allowing both adult and larval activity (Rust and Hanks, 1982). Maximum precipitation during the cold period, with monthly averages above average monthly precipitation for Oct., Dec., Jan., Feb., and Mar. and fall only slightly below in Nov. (Table 1), produces a humid environment for adults and especially immatures developing during this period. Combination of lower temperatures and more precipitation reduces evaporative losses from subsurface sand which prolongs humid conditions, reducing desiccation problems for the winter active species. Hot, dry summers may represent conditions that are physically unsuitable for many of the smaller SO species and only larger (10 mg or more) species can escape by active temporal movements (Holm and Edney, 1973).

The addition of leaves and flowers from deciduous shrubs on the dune (*Eriogonum kearneyi, Chrysothamnus viscidiflorus, Tetradymia tetrameres, Atriplex confertifolia, Psorothamnus polyadenius* and *Psoralea lanceolata*) will be at a maximum during the start of the cold-month period adding to the organic base for the detritivores. Plant materials are trapped in the sand that collects around the stems of the perennial shrubs, the site where most of the winter active species were collected (Rust and Hanks, 1982). The combination of detritus availability, temperature and moisture conditions favorable to both adults and immatures may explain the winter activity period observed in many SO species.

Long distance dispersal characters, wings, of the SO species divide them into two groups: 1) winged and 2) wingless or brachypterous. *Serica* species, *Tetragonoderus pallidus,* and *Philothris* species are winged and capable of flight. *Rhadine myrmecodes, Niptus ventriculus, Edrotes ventricosus, Eusattus muricatus, Lariversius tibialis,* and *Ammobaenetes lariversi* have no wings and *Cardiophorus* species, *Mecynotarsus delicatulus, Aegialia hardyi, Aphodius nevadensis, Coenonycha* species, and *Chilometopon brachystomum* have brachypterous wings and flight is most likely impossible.

The wingless condition of most of the SO species may represent a derived state of recent origin resulting in reduced chances of being blown away from the dune. However, except for *Chilometopon brachystomum,* the wingless tenebrionids belong to genera or tribes that are primatively flightless (Doyen, 1968, 1972; Arnett, 1960). Active sand dunes are limited in their distribution and size in Great Basin and the chances of being blown to a new dune are considered extremely rare. Sand dunes may be viewed in the same manner as remote oceanic islands with respect to the evolution of flightlessness (Darlington, 1943). An individual of *Aegialia crescenta* from Cresent Dune, NV was observed being blown across the dune in a wind storm. The individual was unable to stop itself (unpublished observation). In *Chilometopon brachystomum,* Doyen (1982) found that the brachypterous condition produced wings that still showed distinct anterior venation indicating recent origin. The wings of *Aegialia hardyi, Aphodius nevadensis, Me-*

Table 3. Seasonal distribution of sand obligate Coleoptera species from eight sand dunes in southwestern United States: Sand Mountain Dune (present study): Blow Sand Mountains Dunes, Nevada (Bechtel et al., 1983): Eureka Valley Dune, California; Owens Lake Dune, California; Cadiz Dune, California; Rice Dune, California; Palen Dune, California; and Algodones Dune, California (Andrews et al., 1979). Dunes are arranged latitudinally from north, Sand Mountain, to south, Algodones Dune. Winter (W) November to February, spring (S) March to May, summer (S) June to August and fall (F) September to October (after Andrews et al., 1979).

	Sand				Blow				Eureka				Owens				Cadiz				Rice				Palen				Algodones			
Species	W	S	S	F	W	S	S	F	W	S	S	F	W	S	S	F	W	S	S	F	W	S	S	F	W	S	S	F	W	S	S	F
Mecynotarsus delicatulus	X	X	X	X			X	X			—			X	X			—				—			X	X		X		X		
Tetragonoderus pallidus		X	X				X	X		X	X	X		X		X	X			X		X	X	X	X			X	X	X	X	X
Neptus ventriculus	X	X	X	X	X	X	X	X			—				—		X	X		X	—		X			X		X		X		X
Edrotes ventricosus	X	X	X	X	X	X	X	X	X	X	X	X	X	X			X	X	X	X	X	X	X	X	X	X		X	X	X	X	X
Eusattus muricatus	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X		—		
Lariversius tibialis	X	X	X	X	X	X	X	X	X	X	X			—				—				—				—				—		
Trodloderus costatus	X	X	X	X		X	X		X	X	X	X		X	X	X			X	X			X	X		—				—		

cynotarsus delicatulus, Coenonycha species, and *Cardiophorus* species are reduced to very short paddle-like structure without any trace of venation. This being interpreted as an older condition than that of *C. brachystomum.*

The hypothesis being presented is that the present distributions and restriction of the sand obligate fauna in the southwestern United States is a result of past climatic conditions and contraction of sand areas with decreasing aridity in recent times. This hypothesis is not new; Howden (1963) suggested that distribution patterns observed in eight genera of flightless Scarabaeid beetles found in North America can best be explained by past climatic conditions during the Pre-Pleistocene and Pleistocene periods in non-glaciated areas. La Rivers (1946) also suggested that the subspeciation observed in *Trogloderus costatus* may have been associated with the desiccation of Pleistocene lakes in western Nevada and that *T. costatus nevadus* is confined to the distribution of Lake Lahontan.

The Pleistocene is geologically noted for its glacial record (Flint, 1971) and approximately 15 periods of cooling and warming have been associated with glacial and interglacial periods (Kvasov, 1978). The past 40,000 years in the Great Basin began with an interpluvial period lasting to near 25,000 B.P. Two pluvial periods lasted from 25,000 to 21,500 and 13,600 to 11,100 B.P. with high stands of greater than 1300 m (Benson, 1978; Morrison, 1965). Numerous pluvial lakes, the largest in the western Great Basin being Lake Lahontan (13,580 km^2) (Mifflin and Wheat, 1979), existed throughout the Great Basin. Extensive sand shores and sand deposits were present in the western lakes receiving discharge from the Sierra Nevada Mountains (Morrison, 1964). Warm, arid conditions prevailed from 9000 to 5000 B.P. and during this time all lakes except Pyramid Lake (northwestern Nevada) desiccated and during the last 5000 years Pyramid and Walker lakes (west-central Nevada) have increased in size (Benson, 1978). Pluvial paleoclimates have been estimated as approximately 5°F (2.77°C) cooler than present with a corresponding increase in precipitation averaging 68% above present basin averages (Mifflin and Wheat, 1979).

Present species distributions potentially follow the eolian dispersal patterns of the sands from points of deposition or distribution on pluvial lake shores to its present position. Sand at Sand Mountain is from the Walker River drainage of the Sierra Nevada Mountains (D. Trexler, USGS, Univ. Nevada, Reno, pers. comm.) and has moved from 50 to 55 km to its present position at Sand Mountain. One other active dune, Blow Sand Mountains, lies 25 km SSW of Sand Mountain and is formed from the same sand deposit. All SO species except *Cardiophorus* species, *Aphodius nevadensis* and *Coenonycha* species were present at Blow Sand Mountains (Bechtel et al., 1981, 1983). Presently, we see widespread and/or newly evolved populations of these past faunas trapped in the active sand dunes of the intermountain basins. The widespread species are *M. delicatulus, T. pallidus, N. ventriculus, E. ventricosus, E. muricatus,* and *T. costatus,* with *Ammobaenetes lariversi* and *A. hardyi* and other possible Sand Mountain endemics represent the newly speciated forms. Doyen and Slobodchikoff (1984) have shown the development of microgeographic races of the costal dune beetle *Coelus ciliatus* (Tenebrionidae) from different types of dunes without isolation. Populations inhabiting the eolian and stabilized dunes were among the longest and smallest observed for the species. Doyen and Rogers (1984) found that body size (elytral length and width) in *Eusattus muricatus* was inversely associated with altitude and latitude over a large geographic area and speculate that temperature (annual accumulated day degrees) is involved with body size determination. Whether or not the widespread SO species are genetically different at different dunes within their geographic ranges, it appears that the ephemeral nature of sand dunes may allow for extremely rapid selection and isolation of SO species and populations.

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